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THE LAND SNAIL FAUNA OF A SQUARE KILOMETER PATCH OF RAINFOREST IN SOUTHWESTERN CAMEROON: HIGH SPECIES RICHNESS, LOW ABUNDANCE AND SEASONAL FLUCTUATIONS

A. J. de Winter & E. Gittenberger

Institute of Evolutionary and Ecological Sciences, University of Leiden, c/o National Museum of Natural History, P. O. Box 9517, NL 2300 RA Leiden, The Netherlands; sbu2eg@rulsfb.leidenuniv.de

ABSTRACT

Systematic sampling of a single square km patch of rather acidic, undisturbed, fairly uniform Cameroonian rainforest during two different rainy seasons yielded 97 species of land snails, belonging to at least 12 families. Up to 45 species were collected within a single sampling site of 20 m × 20 m during a single visit, and up to 51 during two visits in different seasons. This might be the world's highest sympatric land snail diversity reported to date. Variation in species composition among the sampling sites appeared to be largely random, and not due to geographic or ecological replacement. Three (super)families make up 86% of the species, the carnivorous Streptaxidae (34%) being the most diverse. Overall snail abundance was rather low, and many species were rare. Of 64% of the species, the abundance was less than 1% of all specimens (2,654) collected. A substantial difference was observed in overall snail abundance between the two sampling periods. About 27% of the species were uniquely found in one of the two sampling periods, and many species differed more than 50% in relative abundance between these seasons. At least 27% of the species were largely or completely arboreal, and 19% were found to live both on the ground and in the vegetation; 46% of the species appear to be confined to the ground, and of 7% insufficient information was available. Major adult shell dimensions (height or diameter) range between approximately 1 and 165 mm, but the vast majority (74%) of species has adult shells smaller than 10 mm. The shell height:diameter ratio distribution is bimodal, but differs from those previously reported for other faunas by relatively many "globose" (H/D 0.8-1.2) and very tall (H/D 2.8-4.4) shells. The distribution of neither shell size nor shell shape differed between ground-dwelling and (partly) arboreal species.

Key words: Gastropoda, Africa, species diversity, biodiversity, species abundance, shell size, shell shape, vertical distribution, seasonal variation.

INTRODUCTION

Tropical rainforests in Africa and elsewhere are severely threatened by commercial timber logging and both slash-and-burn and cash crop agriculture. Huge areas of forest have already been degraded or have disappeared before information could be obtained about their biodiversity and ecology. Originally, closed forests covered large parts of Cameroon. During the period 1980-1990 approximately 140,000 ha (0.6%) were destroyed or degraded annually, and some 40% of the original forest cover now remains (Dixon et al., 1996). In view of the poor economic conditions of the country, there seems to be little hope that this trend will change in the near future. Detailed data on the biodiversity and ecology of undisturbed forest faunas are therefore urgently needed. This information would enable comparisons with various types of degraded forest, enabling, for example, conservation planning and evaluation of the usefulness of future reforestation from the viewpoint of biodiversity restoration. The lack of knowledge of the effects of disturbance on biodiversity is most apparent for invertebrates, including gastropods.

Land snails are a poorly studied group in tropical forests, including those of western Africa. Mainly on the basis of tentative ecological reasoning, Solem (1984) asserted that in rainforests land snails are "generally neither diverse nor abundant." Recent studies have challenged the universality of this statement with respect to species diversity (De Winter, 1992, 1995; Emberton, 1995; Tattersfield, 1996).

The present study describes the land snail diversity in a single square km patch of undisturbed rainforest in southwestern Cameroon in some detail, in order to obtain baseline data for future research in this and other tropical forest regions. Data from disturbed forests in this region will be given in additional papers.

This study is carried out within the framework of the Tropenbos Cameroon Programme (TCP), which was established in 1992 by the Cameroonian Ministry of Environment and Forests (MINEF) and the Dutch Tropenbos Foundation. The general objective of this multidisciplinary programme is to develop methods and strategies for the management of natural forests enabling sustainable, that is, ecologically sound, socially acceptable, and economically viable, production of timber and other products and services (Foahom & Jonkers, 1992). The TCP study area (Fig. 1) covers 1916 km^2, and coincides with two adjacent concessions of a Dutch timber company.

THE STUDY AREA

The 1 km × 1 km patch of undisturbed rainforest studied ("block i2", as indicated on the prospection map of the timber company) is located about 15 km S of Lolodorf (about 3°06′N, 10°44′E; Figs. 1, 2). Block i2 comprises the relatively low and flat southwestern part of the so-called Biboo-Minwo catchment, a study region of c. 7.7 km^2 with an altitude between about 420 and 720 m located in the transition zone between the western lowlands and the eastern, more mountainous, part of the TCP area (Waterloo et al., 1997). Within block i2, elevations range from approximately 420 m in the western and central parts to approximately 480 m in the eastern fringes.

The geology reflects the erosion of the Precambrian shield, the region being dissected by streams and small rivers into undulating plains and remaining hills with bedrock consisting of acid gneisses. The soils are moderately to well drained, with clay and sand contents of about 35% and 45% in the topsoil (upper 0–10 cm), respectively. The topsoil is poor in nutrients (total nitrogen 0.25–0.5%, organic carbon 4–8%, available phosphorous 12–26 ppm), and very strongly to extremely acidic, with pH(H_2O) between 5 and 3.5 (Van Gemerden & Hazeu, in press). Small to very large (up to 5 m high), flat-topped rock outcrops mainly occur in the eastern and southwestern parts of block i2.

Southwest Cameroon forms part of the Guineo-Congolian domain of dense and humid evergreen rainforests. The study site lies within the Biafran Atlantic district, the flora of which is rich in Caesalpiniaceae (Letouzey, 1985). In these forests, four vegetational layers can be distinguished, with gradual transitions. The crowns of the emergent trees, sometimes surpassing 60 m in height, constitute the highest level and cover 20–30% of the ground surface. Canopies of mature trees of 25–40 m high form the second layer, covering 60–80% of the floor surface. The third layer of shrubs and small trees may reach 3–6 m, and the remaining layer of herbs is less than 1 m high. The foliage of the latter two layers covers 40–60% of the floor surface. Lianas are abundant in the canopy and in natural gaps.

The vegetation of the region, including that of block i2, may be classified as very old secondary forest, with perhaps true virgin forest on the steeper hill slopes (Van Gemerden & Hazeu, in press). The sheer size of the trees indicates that it has been left in peace for some centuries. According to Letouzey (1968) the region was subjected to extensive forest clearing by man in the 18th century. Letouzey's (1968) conclusion was based on historical research, as well as on the common occurrence of the tree *Lophira alata* ("Azobé"), the seeds of which germinate best under light conditions. His view seems to be in agreement with the presence in block i2 of a few truly giant *Ceiba pentandra* (with buttresses about 7 m wide), a tree more typical of young secondary forests and arable land. Preliminary data of M. P. M. Parren (pers. comm.) show a substantial tree diversity (diameter at breast height >10 cm) of about 125 species ha^{-1}. The area is relatively rich in valuable timber species, of which especially *Lophira alata* and others such as *Pterocarpus soyauxii* ("Padouk") and *Entandrophragma utile* ("Sipo") are exploited.

The climate is equatorial. The area receives about 2,100 mm precipitation annually, with distinctly wet periods in September-November and in April-May. There is a relatively dry period between December and March, when the monthly rainfall is well below 100 mm. Mean maximum daily precipitation is as high as 115 mm. Relative humidities are high throughout the year, with mean minimum and maximum monthly values of about 70% and 96%, respectively. The air temperature is little variable over the year (mean 24.6°C), with minimum monthly values of approximately 23°C in August and maximum values of approximately 26°C in March. The wind direction is predominantly W-SW, and wind speeds are generally low (less than 4 m s^{-1}); high wind

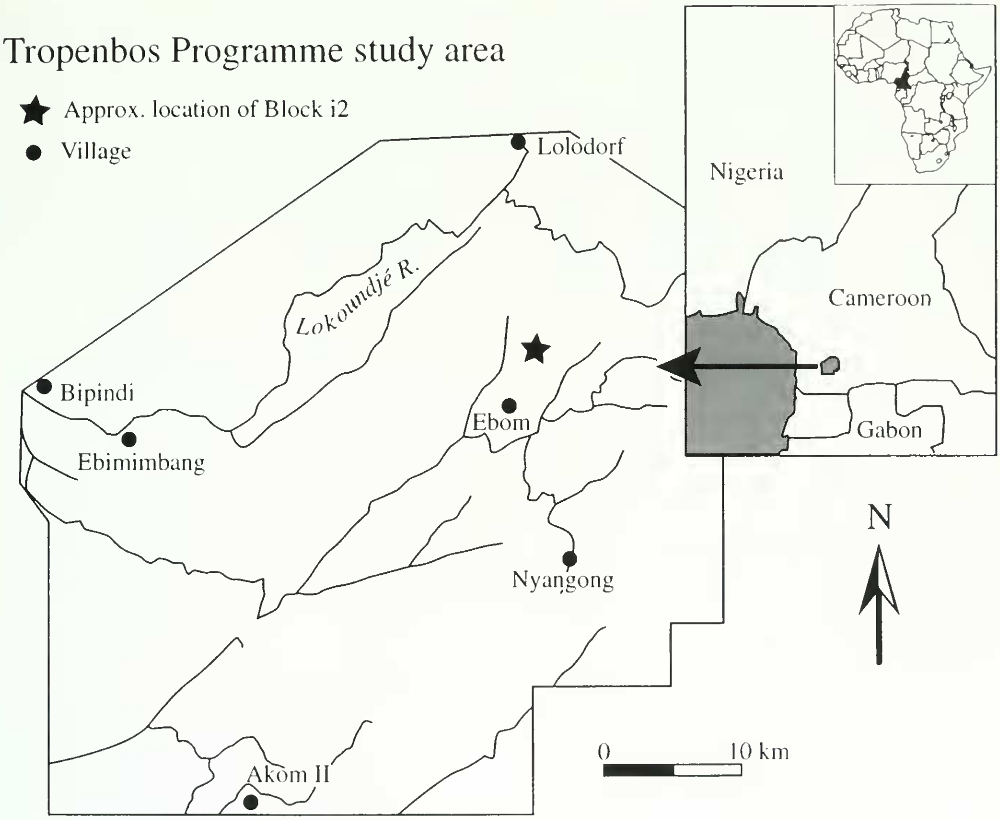

FIG. 1. The location of the square km forest site studied ("block i2") within the area covered by the Tropenbos Cameroon Programme.

speeds can occur during thunderstorms (climatic data, partly extrapolated, from Waterloo et al., 1997).

Although there is variation among the sites sampled in such characteristics as slope inclination and exposition, presence or absence of rock outcrops, and tree species, the overall nature of block i2 appeared to be fairly homogeneous: rivers are less than 5 m wide, and altitude differences are 60 m at most. During the first visit in 1995, the area was still virtually undisturbed, and the canopy closed, except for some natural gaps. However, in February/March 1996 most of the region, including block i2, was selectively logged with an intensity of about 1 tree ha^{-1}. Since the logging activities took place shortly before or during this visit, we assumed that logging could not yet have affected our results, especially since disturbed sites were avoided.

MATERIAL AND METHODS

Sampling

Sampling took place in two periods, August 29–October 6, 1995, and March 21–April 12, 1996, further referred to as "1995" and "1996." Each sampling period was early in one of the two rainy seasons.

Collections were made within patches of 20 m × 20 m that were marked with poles (called "sampling sites", "stations", or "plots" in this paper). Stations on rock boulders were considerably smaller than 20 m × 20 m. In all sites, the actual ground surface thoroughly sampled covered only a small part of the entire site.

In each sampling site, the forest floor was searched for 60 min. In this period samples of leaf-litter and a few mm of topsoil were also taken from several microhabitats that seemed to be favourable for snails, such as beside logs and between roots of trees where dead organic material accumulates. Approximately four litres of litter from each station were sieved in a large cotton bag in which half way down a sieve of 15 mm mesh was secured. The coarse material was searched for larger species on the spot (in small portions on a plate), and the material that passed the sieve was bagged and dried. The volume of the bagged litter varied substantially, depending on the amount of decomposed matter relative to intact surface leaves and twigs on the forest floor. Litter on top of the rock boulders was often more decomposed and contained more humus than that on the forest floor proper.

At many sampling plots, the understorey vegetation (about 3/4 m to 3 m high) was systematically beaten over an open, inverted umbrella. The snails spotted in the umbrella were picked out, and the remaining leaves, twigs and fine material were bagged for later examination. In addition, the trunks of trees were carefully searched for about 30 min. The floor was searched by the senior author, whilst the understorey vegetation and tree trunks were generally sampled by E.-J. Semengue, a well-trained and dedicated local worker.

Because there is only low, herbaceous vegetation on the horizontal top surface of the rock boulders, both persons engaged in hand picking and litter sampling on the rock surface for 60 min. Also some non-boulder sites were incompletely (only the floor or the vegetation) sampled due to various logistic reasons (Table 1). In principle, sites visited in 1995 were sampled again in 1996. However, due to logging activities in 1996 a number of sites sampled in 1995 were disturbed, and new plots were chosen. The exact boundaries of a previously visited plot were not always easy to determine, because the demarcation poles had been removed after the first visit. In order to emphasize that the position of a plot visited for the second time is likely to deviate somewhat from that during the first visit, each sample was given a unique station number. In 1995, 16 sites were studied (including those on rock boulders), whilst 20 sites (including the ones sampled also in 1995) were visited in 1996. The approximate location of the sampling plots is indicated in Figure 2. Table 1 provides details of each station.

In addition, snail shells were extracted from eight litter samples taken for hydrological studies in May 1996 and kindly provided by M. Ruppert. Each of these samples consisted of all the leaf-litter present on a floor surface quadrate of 50 cm × 50 cm. The quadrates were placed randomly with respect to litter quantities within a flat patch of 50 m × 50 m forest floor, but spots with larger pieces of dead wood were avoided. The litter was dried in a stove, passed through a 15 mm mesh sieve, and the snails from the coarse fraction were removed. The fine fraction was retained and further dealt with as described below.

Analysis of Samples

Some months after collecting, the volume of the retained fraction of the floor and boulder litter samples was measured. Then the litter was passed through three sieves (5 mm, 2 mm, and 0.5 mm). The finest fraction was discarded after the first three bags were examined, because it proved to contain no molluscs. From the coarse fraction snails were picked out by eye, whilst the remaining fractions were systematically searched in small portions under a stereo-microscope.

The bagged material from the vegetation was treated in the same manner, but the volume was not measured.

Because of the considerable time interval between collecting and searching of the floor litter samples, the distinction between empty shells and shells that contain a dried-in animal proved to be difficult, especially because occasionally live specimens were observed with strongly eroded shells. In this hot, humid and acidic environment the decomposition of most empty shells (the heavy ones of some Achatinidae perhaps excluded) probably takes less than two months (De Winter, unpublished observations). We therefore decided not to distinguish between live specimens and empty shells in most of the analyses of species diversity and abundance. The relatively few snails spotted in the field were included in the data obtained from the litter, since direct searching took place at the same spots where the litter samples were taken. All snails encountered alive were preserved in ethanol in order to obtain material for future anatomical studies; this collection also served to infer information on the species' preferred habitat.

The snails collected from the tree-trunks proved to belong to the same species as those collected from the understorey vegetation, and were therefore added to these.

In the field no empty shells were found in the vegetation, probably because deceased animals will usually drop to the floor. Virtually

TABLE 1. Annotated list of sampling sites, with station number, date, type(s) of habitat sampled (B, boulder; F, floor; V, vegetation), altitude (in m above sea level), topography, direction of exposition, presence of bare rock (0, none; 1, few minor rocks; 2, large boulders), litter volume (in cc, remaining of 4 litres of litter that passed a 1.5 cm-mesh sieve), as well as numbers of specimens (Nspm) and species (Nspp) in the various habitat types and in total.

Station	Date	Habitat	Alt.	Topogr.	Exp.	Rock	Litter vol.	Nspm (Total)	Nspm (F)	Nspm (V)	Nspp (Total)	Nspp (F)	Nspp (V)	Remarks
007	29/8/95	F	420	flat	—	0	900	21	21	—	9	9	—	
008	29/8/95	F,V	430	faint slope	W	0	1100	102	97	5	31	28	6	large rotting log, old gap
009	30/8/95	F	410	valley	—	0	1000	51	51	—	13	13	—	riverine forest
010	30/8/96	F,V	410	valley	—	0	1500	113	91	22	31	23	12	riverine forest
011	30/8/97	F,V	430	upper slope	N	0	700	39	27	12	21	13	8	steep slope towards stream
012	31/8/95	F,V	420	lower slope	NNE	1	1100	72	47	25	31	16	17	dynamic forest on steep slope
013	31/8/95	B	420	valley	—	2	2100	130	—	—	31	—	—	3–4 m high boulder along stream, top surface sampled 4 × 3.5 m
014	31/8/95	B	470	upper slope	—	2	1900	65	—	—	26	—	—	3–4 m high boulder, top surface sampled 5 × 3 m
015	31/8/95	F,V	470	ridge	—	0	600	30	29	1	14	14	1	
017	19/9/95	B	480	ridge	—	2	1500	71	—	—	29	—	—	3–4 m high boulder, top surface sampled 5 × 3 m, partly sun-exposed
018	19/9/95	F, V	470	upper slope	N	1	2000	135	126	9	22	18	6	
019	20/9/95	F, V	480	upper slope	NNW	1	1400	78	69	9	35	29	8	rel. sparse understorey vegetation
020	20/9/95	B	480	ridge	—	2	1500	103	—	—	26	—	—	3–4 m high boulder, top surface sampled 4 × 4 m, partly sun-exposed
022	21/9/95	F, V	420	flat	—	1	1550	257	61	196	45	28	28	approx. 20 m from gap; dense understory vegetation
024	22/9/95	V	460	gentle slope	N	0	—	31	—	31	14	—	14	due to heavy rain only vegetation sampled
039	6/10/95	F, V	420	flat	—	0	900	64	20	44	20	7	16	

(continued)

TABLE 1. (*Continued*)

Station	Date	Habitat	Alt.	Topogr.	Exp.	Rock	Litter vol.	Nspm (Total)	Nspm (F)	Nspm (V)	Nspp (Total)	Nspp (F)	Nspp (V)	Remarks
055	21/3/96	F, V	470	ridge	—	1	1800	38	27	11	13	10	4	
056	21/3/96	B	470	ridge	—	2	2200	34	—	—	15	—	—	same as sta014
058	22/3/96	F	420	valley	—	0	2100	39	39	—	13	13	—	
059	26/3/96	F, V	480	upper slope	NNW	1	3100	100	68	32	40	37	13	same as sta017
060	26/3/96	B	480	ridge	—	2	1450	41	—	—	16	—	—	same as sta020
061	26/3/96	F, V	460	upper slope	N	1	2550	131	108	23	34	29	10	
062	27/3/96	F, V	410	valley	—	0	1975	76	39	37	30	20	15	same as sta010
063	27/3/96	F, V	420	lower slope	NNE	1	1525	66	44	22	37	28	12	same as sta012
064	27/3/96	B	420	valley	—	2	1700	104	—	—	22	—	—	same as sta013
065	28/3/96	F, V	420	slope	E	1	1550	67	62	5	31	27	4	rocky slope 10 m from natural gap
067	28/3/96	F, V	420	flat	—	0	700	22	11	11	14	9	5	same as sta039
068	4/01/96	F, V	420	flat	—	0	1800	78	38	40	29	20	10	
072	4/03/96	F, V	420	gentle slope	—	0	2100	73	32	41	20	12	9	
073	4/03/96	F, V	430	lower slope	N	0	3200	100	59	41	27	21	9	low understory vegetation; thin litter layer
074	4/04/96	F, V	420	undulating/ flat	—	0	1425	52	30	22	19	12	8	
075	4/4/96	F, V	420	flat	—	0	2250	99	63	36	32	22	12	
076	9/4/96	F, V	430	faint slope	—	0	1100	41	22	19	21	13	10	same as sta008
079	10/4/96	F, V	430	faint slope	—	0	1200	24	11	13	9	6	4	
082	12/4/96	F, V	420	flat	—	0	1250	67	32	35	26	15	11	
083	12/4/96	F, V	420	flat	—	0	1000	40	35	5	21	18	4	dense understorey vegetation; giant *Ceiba* tree

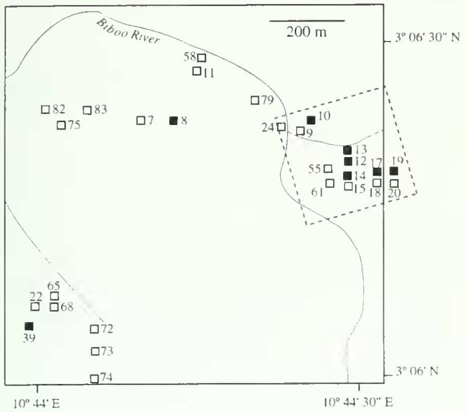

FIG. 2. The approximate location of the sampling sites within the square km forest area studied. Open squares: sites sampled once, either in 1995 or 1996; closed squares: sites sampled in both years. See Table 1 for further details. The dashed line indicates the boundaries of a 9 ha plot used for forestry studies.

all shells extracted from the vegetation litter samples were in a fresh condition and presumably caught alive.

Although in some groups (e.g., most Streptaxidae), it is possible to distinguish between adult and juvenile shells by the morphology of the aperture, most species encountered have an undetermined shell growth, and many can reproduce before reaching their maximum shell size (e.g., Subulinidae). Therefore, we did not distinguish between adult and juvenile specimens in the analyses.

Analysis of Diversity Patterns

The study is of a qualitative rather than a quantitative nature. Although searching time was standardized, and sampling took place within sites not exceeding 0.04 ha, results from different sites are not directly comparable for various reasons. Firstly, due to the heterogeneous structure of the environment, floor litter sampling was not at random, but concentrated on spots that, subjectively, seemed to be favourable for land snails. Secondly, in view of the small overall number of specimens found, and the high proportion of rare species, the presence or absence of many species often seemed to be of a stochastical rather than a systematic nature. Thirdly, numbers of live specimens obtained, especially of arboreal species, often varied greatly between days, and even within days. This seemed to be due to variation in climatic conditions, especially humidity and temperature, rather than to ecological differences between sites. Differences in circadian activity patterns of the species may also have had an effect; nocturnal species are more likely to be found early in the morning. In view of these limitations, elaborate statistical analyses of our data with respect to both species composition and abundance appeared to be of little value. However, data were sufficient to detect some general trends.

The measures of diversity used in this study are overall species richness (S), and Whittaker's index I, which is the total number of species recorded (S) divided by the mean number of species per site (α), providing a measure of diversity difference among sites (Magurran, 1988; Cameron, 1992). If I equals 1, sites have identical faunas, and higher values indicate increasing differentiation. High values of I can result from geographical or ecological replacement of taxa, or from chance effects due to sampling error. These patterns can be distinguished by comparing the variance of sites per species to the maximum variance possible for the same values of S and α, as explained in Cameron (1992). If the achieved variance is low, replacement effects will be more important than chance effects, and vice versa.

Identification and Taxonomy

The vast majority of the species were classified according to shell characters only, except for the urocyclid slug-like taxa (*Zonitarion, Verrucarion*), of which one adult specimen per sample, if available, was dissected. This means that the estimates of the numbers of species might be conservative; additional cryptic species may be present, especially among the shelled Urocyclidae. In view of the small size and overall homogeneous nature of the area studied, it seems improbable that the number of species was overestimated as the result of intraspecific variation in shell characters.

The taxonomy and distribution of most land snails in Cameroon and elsewhere in western Africa are poorly known. Most names used in this study are provisional. The use of "cf." in a name merely serves to point out a resemblance to a described species. Virtually all juvenile shells could be assigned to a species by careful comparison of spire dimensions and sculpture, especially of the embryonic whorls. A few juvenile shells that could not be matched with adult specimens of species already recognised were treated as separate species. Most species were assigned to known genera, but it should be kept in mind that many of these probably comprise a heterogeneous assemblage of species that are more or less similar in shell characters. The anatomy of species described from western Africa, including type species of genera, is generally not or insufficiently known.

RESULTS

Faunal Composition

Table 2 lists the 97 species recognised in this study, 34 of which are probably previously described, 22 seem to be new to science, and 41 are of unclear status. A substantial portion of the latter group might be undescribed as well. The distributions of all 34 described species, as well as of a fair number of the remaining ones, extend well beyond the Biboo-Minwo region.

The species found in this study belong to at least 12 families, two of which are Prosobranchia Mesogastropoda, the remaining Pulmonata (Soleolifera and Stylommatophora) (Table 3). The family assignment of some species is at best tentative in the absence of anatomical data.

The fauna is dominated by three (super)-families, the Streptaxidae (33 species), the Achatinoidea (27 species, the majority being subulinids), and the Helicarionoidea (23 species). Together they constitute 86% of the species observed. The Streptaxidae are carnivores, the other two are vegetarians *sensu lato,* as far as is known.

Streptaxids were both surprisingly speciose and abundant, comprising 33 (34%) of the species observed and 29% of all individuals collected. *Gulella (Paucidentina)* sp. 1 was the most common species in this study, contributing about 10% of all specimens found and present in virtually all sites. Streptaxidae were comparatively less diverse and less abundant in the collections from the vegetation (25% of the species, 18% of the individuals) than in those from the forest floor (35% of the species and 33% of the individuals).

Species Diversity and Abundance

Of the 97 species recorded from the entire 100 ha area, 80 were found in 1995, nine of which were not encountered again in 1996. Of the 88 species observed in 1996, 17 were not found in 1995. High species richness was also found in smaller areas. An intensively studied subarea of 300 m × 300 m (13 sites sampled, 6 of which sampled in both seasons; Fig. 2), one of several 9 ha plots marked in the field for forestry studies and used by us for orientation, yielded 83 species, 67 of which were obtained in 1995, and 74 in 1996.

Species diversity and abundance data of the sampling sites are summarized in Table 1. The complete data table of the species and numbers of specimens per station will be deposited in the archives of the National Museum of Natural History, Leiden. The highest diversity found during a single visit (in 1995) of a 20 m × 20 m sampling site (Sta022) was 45 species, which represents 56% of all species found in 1995 and 46% of the total fauna observed in both seasons. Unfortunately, this site was disturbed in 1996 and could not be resampled. Instead, a seemingly similar site approximately 25 m to the east (Sta068) was sampled; together these two sites yielded 57 species, or 59% of the total number of species observed in block i2. The "revisited" stations comprised five plots, of which both the floor and the vegetation were sampled, and three rock boulder sites (Table 1, Fig. 2). The total number of species found during both sampling periods varied between 27 and 51 (mean 42.2) species among the floor-plus-vegetation plots, and between 29 and 39 (mean 33.3) species among the boulder sites.

The diversity patterns were quantitatively analysed for stations of which both the floor and the vegetation were sampled, as well as for collections from the major habitat types (floor, vegetation, rock boulders) separately (Table 4).

The floor-plus-vegetation sites (eight in 1995, 16 in 1996, including five "revisited" plots) yielded 95 of the 97 species observed (76 in 1995, 86 in 1996). For both years, the Whittaker's index *I* indicates substantial variation in species diversity between the stations. The proportion of the maximum possible variance achieved for stations per species was not indicative of significant replacement of species (cf. values given in Cameron, 1992; Tattersfield, 1996). Whittaker's index values

TABLE 2. List of 97 land snail species recorded in one square km of rainforest in SW. Cameroon, with numbers of specimens collected in 1995 and 1996. Species are ordered according to total number of specimens collected. Tentative type of habitat (vertical distribution) is indicated as A (arboreal), F (floor-dwelling), I ("indifferent") or ? (unknown). In the absense of anatomical data for most species, the Charopidae/Punctidae are united in the superfamily Punctoidea, the Subulinidae/Ferussaciidae are grouped with the Achatinidae in the Achatinoidea, and the Euconulidae, Urocyclidae and related (sub) families in the Helicarionoidea. If possible, the tentative family assignment is also indicated.

SPECIES	FAMILY	Number 1995	Number 1996	Total	Habitat
Gulella (*Paucidentina*) sp. 1	Streptaxidae	142	128	270	F
Pseudopeas sp. 2	Achatinoidea/Subulinidae	93	61	154	F
Trochozonites cf. *pilosus* d'Ailly	Helicarionoidea/Urocyclidae	91	40	131	I
Zonitarion semimembranaceus (Martens)	Helicarionoidea/Urocyclidae	71	47	118	A
Afropunctum sp.	Helicarionoidea/Euconulidae	43	72	115	A
Dictyoglessula sp.	Achatinoidea/Subulinidae	54	52	106	F
Philalanka cf. *delicatula* Thiele	Punctoidea	20	62	82	A
Pseudopeas sp. 3	Achatinoidea/Subulinidae	31	48	79	A
Trochozonites sp. 2	Helicarionoidea/Urocyclidae	15	63	78	A
Thapsia cf. *troglodytes* (Morelet)	Helicarionoidea/ Urocyclidae	42	30	72	I
Gulella bolocoensis Ortiz & Ortiz	Streptaxidae	38	26	64	F
Cyathopoma n.sp.	Cyclophoridae	48	14	62	F
?Endodontoid n.gen. n.sp. 2	Punctoidea	32	30	62	F
Kaliella sp.	Helicarionoidea/Euconulidae	39	23	62	I
Trochozonites cf. *bifilaris* (Dohrn)	Helicarionoidea/Urocyclidae	36	14	50	I
Gulella feai Germain	Streptaxidae	35	14	49	F
Nesopupa bisulcata (Jickeli)	Vertiginidae	26	20	46	F
Curvella sp. 1	Achatinoidea/Subulinidae	27	13	40	F
Ptychotrema (*Ennea*) *silvatica* Pilsbry	Streptaxidae	28	12	40	F
Ischnoglessula sp. 1	Achatinoidea/Subulinidae	20	17	37	I
Pseudopeas sp. 1	Achatinoidea/Subulinidae	16	21	37	I
Pileata sp. 1	Achatinoidea/Subulinidae	9	25	34	F
Gulella (*Avakubia*) *acuminata* Thiele	Streptaxidae	12	22	34	A
Pseudoglessula sp.	Achatinoidea/Subulinidae	13	20	33	F
Curvella sp. 2	Achatinoidea/Subulinidae	12	21	33	F
Trochozonites sp. 4	Helicarionoidea/Urocyclidae	25	8	33	F
Achatina iostoma (Pfeiffer)	Achatinoidea/Achatinidae	28	2	30	I
Micractaeon koptawelilense (Germain)	Achatinoidea/? Ferussaciidae	9	21	30	F
Gudeella' sp. 1	Helicarionoidea/Urocyclidae	5	25	30	I
Maizaniella (*Spirulozania*) n.sp.	Maizaniidae	14	15	29	F
Gulella (*Pupigulella*) *pupa* Thiele	Streptaxidae	15	14	29	I
Subulona sp.	Achatinoidea/Subulinidae	9	19	28	F
Streptostele sp. 3	Streptaxidae	10	14	24	F
Ptychotrema (*Ennea*) cf. *aillyi* Adam	Streptaxidae	7	16	23	A
Afroguppya sp. 1	Helicarionoidea/Euconulidae	14	9	23	F
Ischnoglessula sp. 2	Achatinoidea/Subulinidae	15	7	22	A
Gulella (*Avakubia*) cf. *avakubiensis* Pilsbry	Streptaxidae	11	11	22	A
Ptychotrema cf. *columellaris* (Martens)	Streptaxidae	11	10	21	F
Aillya sp. 1	Aillyidae	20	1	21	F
Maizaniella (*Macromaizaniella*) *preussi* (Martens)	Maizaniidae	12	8	20	F
Gulella cf. *suturalis* Degner	Streptaxidae	9	10	19	A
Ptychotrema (*Excisa*) *duseni* (d'Ailly)	Streptaxidae	4	15	19	F
Aillya sp. 2	Aillyidae	19	0	19	F
Ptychotrema (*Ennea*) cf.		10	8	18	I
perforatum (d'Ailly)	Streptaxidae	8	10	18	A
Edentulina liberiana (Lea)	Streptaxidae	4	12	16	F
Gulella (*Costigulella*) n.sp.	Streptaxidae	12	4	16	I
Prositala cf. *butumbiana* (Martens)	Punctoidea				

(*continued*)

TABLE 2. (*Continued*)

SPECIES	FAMILY	Number 1995	Number 1996	Total	Habitat
?Endodontoid n.gen. n.sp. 1	Punctoidea	7	8	15	F
Afroguppya sp. 2	Helicarionoidea/Euconulidae	5	10	15	F
Trochozonites sp. 7	Helicarionoidea/Urocyclidae	8	6	14	A
Trochozonites sp. 8	Helicarionoidea/Urocyclidae	6	7	13	A
Gulella (*Avakubia*) n.sp.	Streptaxidae	4	8	12	A
Trochozonites sp. 1	Helicarionoidea/Urocyclidae	11	1	12	A
Callistoplepa shuttleworthi (Pfeiffer)	Achatinoidea/Achatinidae	5	6	11	I
Gulella (*Conogulella*) sp.	Streptaxidae	3	8	11	I
Streptostele sp. 2	Streptaxidae	4	7	11	F
Pupisoma sp.	Vertiginidae	3	7	10	I
Gulella cf. *germaini* Connolly	Streptaxidae	0	9	9	F
Streptostele sp. 1	Streptaxidae	4	5	9	F
Gulella (*Paucidentina*) sp. 2	Streptaxidae	2	6	8	F
Pileata sp. 2	Achatinoidea/Subulinidae	5	1	6	F
Sinistrexcisa cameruniae De Winter, Gomez & Prieto	Streptaxidae	0	6	6	F
Trochozonites sp. 6	Helicarionoidea/Urocyclidae	2	4	6	A
Gonaxis camerunensis (d'Ailly)	Streptaxidae	2	3	5	F
Pseudoveronicella sp.	Veronicellidae	0	5	5	I
Archachatina marginata (Swainsson)	Achatinoidea/Achatinidae	2	2	4	I
Pseudachatina cf. *downesii* (Gray)	Achatinoidea/Achatinidae	0	4	4	A
Subulina sp.	Achatinoidea/Subulinidae	2	2	4	A
Pseudopeas sp. 4	Achatinoidea/Subulinidae	0	4	4	?
Gulella (*Paucidentina*) cf. *conica* (Martens)	Streptaxidae	2	2	4	I
Ptychotrema (*Ennea*) cf. *complicatum* (Martens)	Streptaxidae	1	3	4	F
Gudeella sp. 2	Helicarionoidea/Urocyclidae	0	4	4	F
Verrucarion sp.	Helicarionoidea/Urocyclidae	3	1	4	A
Trochozonites sp. 9	Helicarionoidea/Urocyclidae	0	4	4	A
Trochozonites sp. 10	Helicarionoidea/Urocyclidae	0	4	4	A
Gulella/*Ennea* spec.	Streptaxidae	1	2	3	?
Edentulina martensi (Smith)	Streptaxidae	2	1	3	F
Streptostele sp. 5	Streptaxidae	0	3	3	F
Trochozonites cf. *adansoniae* (Morelet)	Helicarionoidea/Urocyclidae	0	3	3	A
Trochozonites sp. 5	Helicarionoidea/Urocyclidae	2	1	3	F
Ischnoglessula sp. 3	Achatinoidea/Subulinidae	0	2	2	A
Pseudopeas cf. *feai* Germain	Achatinoidea/Subulinidae	0	2	2	F
Gulella cf. *fernandensis* Ortiz & Ortiz	Streptaxidae	2	0	2	F
Streptostele sp. 4	Streptaxidae	1	1	2	F
Trachycystis cf. *iredalei* (Preston)	Punctoidea	2	0	2	A
Trochozonites sp. 3	Helicarionoidea/Urocyclidae	1	1	2	A
Archachatina camerunensis d'Ailly	Achatinoidea/Achatinidae	1	0	1	A
Lignus solimanus (Morelet)	Achatinoidea/Achatinidae	1	0	1	A
Leptocala mollicella (Morelet)	Achatinoidea/Achatinidae	1	0	1	I
Kempioconcha sp.	Achatinoidea/Subulinidae	1	0	1	F
Opeas sp.	Achatinoidea/Subulinidae	0	1	1	?
?Ferussaciidae/Subulinidae sp.	Achatinoidea	0	1	1	?
Gulella n.sp.	Streptaxidae	0	1	1	?
Ptychotrema (*Parennea*) n.sp.	Streptaxidae	1	0	1	F
?*Gonaxis* spec.	Streptaxidae	1	0	1	?
?Endodontoid n. gen. n. sp. 3	Punctoidea	0	1	1	?
Zonitarion sp. 1	Helicarionoidea/Urocyclidae	0	1	1	F
Totals		1,362	1,292	2,654	

TABLE 3. Systematic list of (super)families and species numbers of land snails found in one square km of rainforest in southwestern Cameroon and their tentative vertical distribution.

		VERTICAL DISTRIBUTION			
Taxon	No. Species	Floor	Arboreal	"Indifferent"	Unknown
PROSOBRANCHIA					
MESOGASTROPODA					
Cyclophoridae	1	1	—	—	—
Maizaniidae	2	2	—	—	—
PULMONATA					
STYLOMMATOPHORA					
Vertiginidae	2	1	—	1	—
Achatinoidea	27	11	7	6	3
Achatinidae	7	—	3	4	—
Subulinidae	18	10	4	2	2
?Ferussaciidae	2	1	—	—	1
Streptaxidae	33	20	6	4	3
Punctoidea	6	2	2	1	1
Aillyidae	2	2	—	—	—
Helicarionoidea	23	6	12	5	—
Euconulidae	4	2	1	1	—
Urocyclidae	19	4	11	4	—
GYMNOMORPHA					
SOLEOLIFERA					
Veronicellidae	1	—	—	1	—
TOTALS	97	45	27	18	7

for samples from the floor and vegetation separately are somewhat greater than for floor-plus-vegetation plots, whilst those for the boulder sites are smallest.

Most species occurred in low numbers (Table 2). Both in 1995 and 1996, 64% of the species were represented by less than 1% of all specimens obtained, about one third took up 1-5%, and only a few species were more common.

Snail abundance was generally low. Collections from all stations in 1995 and 1996 together yielded 2,654 specimens. There was considerable variation among plots and habitats (forest floor, vegetation, boulder) in the number of specimens collected (Table 4). Boulder sites tended to yield more individuals than sites on the forest floor proper, but these differences disappear if abundance is expressed as snails per litter volume. The greater number of specimens collected from rock boulders might be at least partly due to the greater volume of boulder litter sampled, because boulder litter was generally more decomposed, and thus finer, than that on the forest floor. Numbers of snails collected from the arboreal habitats also varied greatly, which seemed to be strongly dependent on weather conditions.

The eight litter samples from 0.25 m^2 (50 cm $\times$ 50 cm) floor quadrates collected in 1996 give an impression of the magnitude and variation of snail density, species richness, and amount of leaf-litter per surface unit of forest floor (Table 5). The data illustrate some characteristic features of this forest: (1) the variability in the amount of (partly decomposed) litter on the forest floor; (2) the low abundance of snails (12–52 snails/m^2 of forest floor, 8–20 shells/l sieved litter); (3) the low specimens:species ratio; and (4) the high species diversity. Comparison of the abundance data of these randomly taken samples (Table 5) with those provided in Table 1 and Table 6 suggests that the *average* snail density per surface unit of forest floor is generally lower than appears from the data of the 0.04 ha sites, which are based on choice litter taken from seemingly favourable microhabitats.

Differences Between Sampling Periods

The total number of specimens found in both seasons was about the same (1,362 in 1995, 1,292 in 1996), but, due to the greater number of sites sampled in 1996, mean number of specimens per site was considerably smaller than in 1995 (Table 4). The total number of species found in 1995 (80) was smaller than in 1996 (88). Mean number of sites per species was relatively greater in 1995 than in 1996.

TABLE 4. Abundance and species diversity statistics of sites located within a square km patch of rainforest in southwestern Cameroon sampled in 1995 and 1996. Data are given for all sites of which both the floor and vegetation (F + V) were sampled, for all floor (F) and vegetation (V) samples separately, as well as for sites on rock boulders (B).

	F + V 1995	F + V 1996	F + V 95 + 96	F 1995	F 1996	F 95 + 96	V 1995	V 1996	V 95 + 96	B 1995	B 1996	B 95 + 96	All
No. sites	8	16	24	11	17	28	9	16	25	4	3	7	36
Total species (S)	76	86	95	64	78	87	41	36	51	47	33	54	97
Total specimens	830	1064	1894	640	720	1360	353	393	746	369	179	548	2654
Specimens/site													
Mean	103.7	66.5	78.9	58.2	42.3	48.6	39.2	24.6	29.8	92.2	59.7	78.3	
S.D.	66.6	29.9	47.9	32.1	23.9	29.1	60.1	13.0	36.9	30.2	38.5	35.4	
Range	39–257	22–131	22–257	20–126	11–108	11–126	5–196	5–41	5–196	65–130	34–104	34–130	
Species/site													
Mean (α)	29.5	25.1	26.6	18	17.8	17.9	12.7	8.7	10.2	28	17.7	23.6	
S.D.	8.6	9.0	8.9	7.9	7.2	7.3	7.2	3.6	5.4	2.4	3.8	6.2	
Range	20–45	12–40	12–45	7–29	6–29	6–31	5–28	4–15	4–28	26–31	15–22	15–31	
/ Whittaker (S/α)	2.6	3.4	3.6	3.5	4.4	4.9	3.2	4.1	5.0	1.7	1.9	2.3	
Sites/species													
Mean	3.1	4.7											
Variance	4.25	12.87											
Maximum var.	10.23	41.45											
% achieved	41	31											

TABLE 5. Snails from a 0.5 m × 0.5 m floor surface quadrat, with the number of species and specimens, the volume of sieved litter, and the number of specimens per litre and per m^2.

	Number of species	Number of shells	Litter vol. (litres)	Shells/ litre of litter	Shells/ m^2
Sample					
1	10	13	0.9	14.4	52
2	5	6	0.3	20.0	24
3	2	3	0.25	12.0	12
4	4	5	0.25	20.0	20
5	4	4	0.5	8.0	16
6	4	4	0.35	11.4	16
7	4	4	0.25	16.0	16
8	6	7	0.4	17.5	28
Totals	22	46	3.2	—	—
Mean	4.9	5.7	0.4	13	23

For many species, the number of specimens per species varied considerably between the two sampling periods (Table 2). Histograms of species frequencies ordered according to decreasing relative abundance (% of total specimens) describe a hollow curve both for 1995 and 1996, but the ranking order of the species in 1995 differed considerably from that in 1996 (Fig. 3). More than one-fourth (26) of the species was found uniquely either in 1995 or in 1996. Of 25 of the species found in both seasons, the relative abundance differed 50% or more between years. *Achatina iostoma*, for instance, was represented in 1995 by three adult shells and 25 juveniles of about 20–30 mm, whilst in 1996 only two adult specimens were encountered. Of *Trochozonites* cf. *pilosus* and *T.* cf. *bifilaris* only clearly juvenile shells were observed in the 1996 samples, whereas both adults and juveniles occurred in much larger numbers in 1995. Only one out of 40 specimens of the two *Aillya* species found was collected in 1996. Such data are suggestive of a life cycle of one year or less. The relative abundance of 46 species differed less conspicuously between years.

For both floor and boulder sites, the absolute number of individuals found per site was generally higher in 1995 than in 1996. However, the mean number of species in the floor sites did not differ between the two sampling periods, whilst in the boulder sites mean species richness was much greater in 1995 (Table 4). This general trend was also observed by comparisons of the eight sites that were sampled in both seasons. The number of individuals per species in the floor samples was significantly lower in 1996 than in 1995, whereas these ratios were the same in the boulder sites (Table 1).

Standardized per litter volume, the median number of specimens in 1995, calculated over all floor and boulder litter samples, was significantly higher than in 1996 (Table 6; one-tailed Mann-Whitney test, $Z = 3.92$, $P = 4.5 \times 10^{-5}$), as was the median number of species (Table 6; one-tailed Mann-Whitney test, $Z = 3.12$, $P = 0.91 \times 10^{-3}$). The larger total number of species found in 1996 might be due to the larger number of sites sampled, and the almost double total volume of (sieved) floor litter taken in that year, increasing the chance of finding new, rare species.

Values of Whittaker's index *I* for 1995 and 1996 (Table 4) indicate that differences in species diversity among sites were greater in 1996 than in 1995. This might well be related

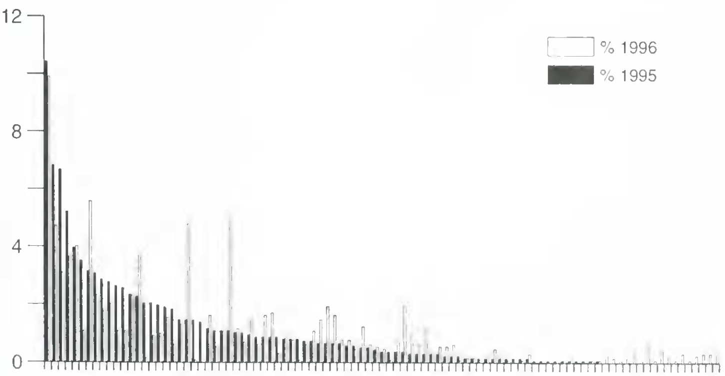

FIG. 3. Relative abundance (% of the total number of specimens collected in each season) of 97 land snail species in 1995 and 1996, ordered according to decreasing abundance in 1995.

TABLE 6. Gastropod diversity and abundance in litter samples taken from the forest floor and from rock boulder in 1995 and 1996, expressed as number of specimens or species per litre of sieved litter.

	Median	Range	Nsamples	Total litter volume	Total specimens
Specimens/litre					
1995	49.3	22.2–88.2	15	19.75	1009
1996	21.1	9.2–61.2	20	36.2	899
Species/litre					
1995	15.3	7.7–25.4	15		
1996	10.6	5.0–18.4	20		

to the lower number of specimens per station in 1996 (Table 4), and thus partly result from sampling error.

Vertical Distribution

The fauna appeared to be stratified with species confined to the ground, species confined to arboreal habitats, and species inhabiting both levels. A majority of 45 species (46%) were classified as floor dweller (F), on evidence that live specimens were almost exclusively found on the forest floor and on boulders, or because specimens of (minute) species commonly found in the floor litter were never obtained from the vegetation. This class includes seven species that were normally encountered on the floor, but of which the odd specimen was found in samples from the vegetation. Species of which live specimens were only found in the vegetation at 3/4 m or more above the ground (27 species, 28%) were considered to have arboreal habits (A), assuming that the relatively few shells found on the forest floor were from deceased animals that had dropped to the ground. The remaining snails that were regularly found alive (18 species, 19%), were classified as "indifferent" (I). Information on the vertical distribution of some uncommon species could be derived from nearby undisturbed forest sites not covered in this report. Of seven species (7%) insufficient information was available. The tentative vertical distribution of the individual species is listed in Table 2.

All major families have representatives in the three classes (F, A, I) recognised (Table 3), only the Achatinidae have no true floor-dwelling species. The majority of the Subulinidae and Streptaxidae species are ground dwellers, whilst of the Urocyclidae significantly more species have arboreal habits.

The upper, horizontal surface of the large rock boulders constitutes a special habitat. Five to 15 m^2 of horizontal rock surface yielded up to 31 species during a single visit (Table 4). Despite intensive searches, snails were never observed on the steep flanks of the 3-5 m high outcrops. Although these rocks are virtually devoid of higher vegetation, a relatively significant proportion of the shells found in the litter belongs to arboreal species. There are usually one or more spots where the woody understorey vegetation grows against the flanks of the boulder, often attached to it by climbers. Possibly some arboreal species migrate between the vegetation and the rock habitat, the microclimates of which might resemble each other.

The occurrence of a limited number of species, such as *Cyathopoma* n. sp.,. *Ptychotrema* (*Ennea*) *silvatica, Gulella bolocoensis, Gulella* (*Costigulella*) n. sp., and *Gulella* (*Pupigulella*) *pupa*, might be associated with the presence of bare rock, but none were confined to the giant boulders.

Shell Size and Shape

Shell height (H) and diameter (D) were measured from an "average" adult specimen of each of 86 species, (semi-)slugs and species known by only juvenile shells being excluded. H ranges between 0.8 and 165 mm, D between 0.9 and 94 mm. Figure 4 gives the distributions of H and D. Major shell dimension (H or D) of 32 species (37%) is less than 5 mm, and of another 32 species (37%) between 5 and 10 mm. Shells of eight species (9%) measure between 10 and 20 mm, and those of 14 species (16%) are larger than 20 mm, four of which have adult shell heights exceeding 90 mm.

Ground-dwelling species did not differ in major shell dimension (H or D) from the arboreal (two-tailed Mann-Whitney test, $Z = 1.12$, $P = 0.26$), "indifferent" ($Z = 1.64$, $P = 0.10$), or arboreal plus "indifferent" species ($Z = 1.65$, $P = 0.10$).

We examined the shell shape distribution of the floor-dwelling, arboreal and "indifferent" species separately, as well as that of these

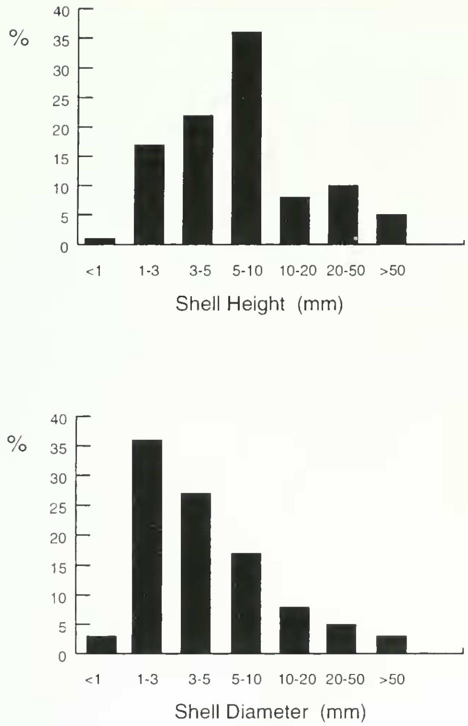

FIG. 4. Shell height (upper graph) and shell diameter (lower graph) distributions of 86 land snail species found within one square km of Cameroonian rainforest.

three groups together (Fig. 5). All distributions in Figure 5 are bimodal, due to relatively many species with "globose" (H/D 0.8–1.2) and moderately tall to very tall shells (H/D > 1.6). Of 82 species, H:D ratios were calculated, excluding six slug-like species (two *Zonitarion*, one *Verrucarion*, one *Pseudoveronicella*, and two *Aillya*), and nine species with unknown vertical distributions or with only juvenile shells available. The H:D ratio distribution of the floor-dwelling species did differ from neither that of the arboreal species (two-tailed Mann-Whitney test, $Z = 1.26$, $P = 0.21$), nor that of the "indifferent" species ($Z = 1.01$, $P = 0.31$) or the arboreal and "indifferent" species together ($Z = 1.42$, $P = 0.15$).

DISCUSSION

Species Richness

The malacofauna of this small patch of acid rainforest was found to be extremely rich in species. Although comparisons with other studies are hampered by a lack of standardisation with respect to area size and sampling methods, this Cameroonian area might well be the globally most species-diverse locality known with respect to land molluscs. The richest site reported so far is Waipipi Reserve, Manakau Peninsula, New Zealand. Solem et al. (1981) reported 60 species from this 4 ha site, and a total number of 72 native species from a surrounding area of approximately 50 × 15 km (but see Emberton (1985) for somewhat lower numbers). Other species-rich sites (all approx. 4 ± 2 ha) include Pine Mountain, Kentucky, U.S.A., where L. Hubricht collected 44 species, and a patch of lowland rainforest near Manombo Village, Fianarantsoa Province, Madagascar, where 52 species were found (both sites described in Emberton, 1995). Tattersfield (1997) reported 50 species from 27

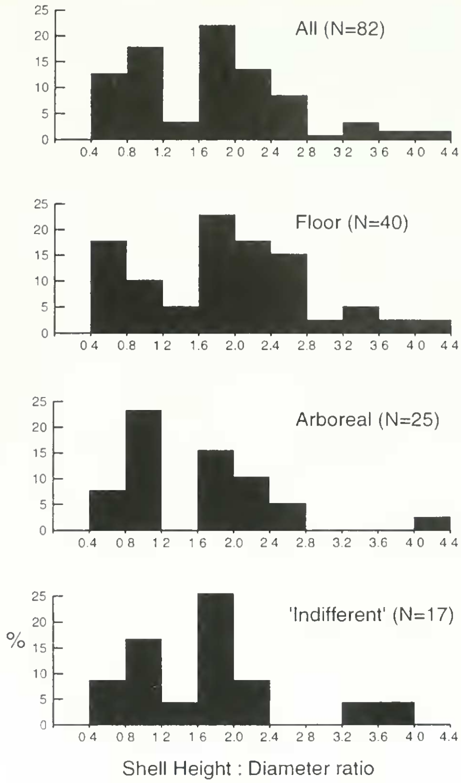

FIG. 5. Shell height:diameter ratio distributions of 82 land snail species found within one square km of Cameroonian rainforest (upper graph), as well as of the floor-dwelling, arboreal and "indifferent" species separately.

plots of 40 m × 40 m each in Kakamega Forest, an area of approximates 265 km^2 in western Kenya, the richest of which yielded 33 species. In this paper, we report 97 species in 100 ha of rainforest, 83 species within a 9 ha subarea, up to 45 in a sampling site of 20 m × 20 m during a single visit, and up to 51 species in sites sampled twice. In all cases, the actual floor surface sampled is much smaller than 0.04 ha. Up to 10 species were found in litter from a 0.5 m × 0.5 m plot.

In view of the large proportion of rare species, it is likely that the actual number of species will even be greater than 97. Several parametric and non-parametric methods have been developed to estimate the actual species richness in similar situations, based on the frequency of rare species in a sampling program. According to Colwell & Coddington (1995) the Chao-2 and second-order Jackknive estimators provide the least biased estimates of true species richness for small numbers of samples. Both estimators are based on presence-absence data, and take into account the number of species that occur in only one or in two samples. These two methods were applied to all stations in 1995 (8) and 1996 (16) of which both the forest floor and vegetation were sampled. The total number of species observed in these plots was 95. The Chao-2 and second-order Jackknive estimates are 107 and 110 species, respectively. Subtracting the two species found in the remaining samples, there may be at least 105–108 species present in this 100 ha area, especially since these non-parametric estimators usually underestimate the true species richness (Colwell & Coddington, 1995).

Possible Explanations for the High Species Diversity

Of the factors favouring high land snail diversity that were discussed by Solem (1984), three might be involved in the situation described here: leaf-litter characteristics, lack of disturbance for prolonged periods of time, and stable moisture supply.

Leaf-litter associated parameters are likely to be important for the high species diversity observed. The majority of species found are floor dwellers, but since leaf-litter occurs also patchily on the understorey vegetation above the forest floor, these factors might also affect certain arboreal taxa. With more than 125 species of trees per ha, the composition and architecture of litter deposits are obviously highly variable. Leaf-litter is unequally distributed on the forest floor, and thicker litter accumulations seemed to contain more individuals and species than spots with thin litter deposits, as was also found by Solem et al. (1981) in New Zealand. Even in tropical evergreen forests trees periodically shed their leaves, but not synchronised like in temperate regions (e.g., Medway, 1972; Hladik, 1978). Thus, thickness, distribution and composition of litter layers are dynamic in both space and time. The great variety in size, shape and firmness of the leaves, combined with differential decomposition rates by spot differences in microclimate, moisture and soil conditions, potentially provides a wide array of microhabitats supporting a high land snail diversity of vegetable matter and fungi consumers, and associated predator species. These factors might partly be involved in the apparent seasonality of the snail fauna observed that might otherwise not be expected in an evergreen forest.

There are only few published reports supporting the view that litter parameters are related to land snail species diversity, for example, those by Solem et al. (1981) on New Zealand, and by Getz & Uetz (1994) on North American forests. Solem's (1984) assertion that rainforests have negligible litter deposits and, therefore, support a little diverse land snail fauna certainly does not hold for the forests of western Africa.

The fauna of this small area is also diverse in taxa above the species level, and seems to include few species that are closely related (as judged largely from conchological characters). The species belong to a considerable number of (sub)genera. Several of the larger generic entities used here are actually composed of various, as yet largely unnamed, distantly related genera. For example, anatomical studies have revealed that *Trochozonites,* the most speciose genus found, is an artificial taxon embracing at least four groups of species, despite their similarity in shell characters (Ortiz de Zárate, 1951). Local speciation therefore seems to have contributed little to the high species richness observed. It is much more probable that this land snail fauna gradually accumulated in the area, possibly over long periods of time.

In the dry and relatively cold glacial periods, the size of the African forest belt was much reduced to a small number of discrete areas.

The study area is situated within such a putative Pleistocene forest refugium (Maley, 1996). Whether this is in any way related to the high actual species richness can only be investigated by comparison with other areas, both within and outside the hypothesized refugia.

Absence of stress periods by prolonged droughts probably favours high species diversity, because the moisture regime determines the possible activity periods of land snails (Solem et al., 1981). Even in the driest periods of the year the study area receives up to 80 mm precipitation per month (Waterloo et al, 1997). According to Solem (1984) rainforests suffer from too much rain, which causes leaching of nutrients, and are therefore little diverse in land snails.

If the proportion of arboreal species in this fauna is truly greater than in other faunas, this might also be a factor contributing to the high species diversity. Waipipi Reserve in New Zealand had only 14 out of 60 species with arboreal habits, including several which live both on the floor and in the vegetation (Solem et al., 1981; Solem & Climo, 1985). There appear to be hardly any published data on the number of arboreal species in other faunas, however. Most studies appear to have adopted sampling techniques that underestimate the numbers of arboreal taxa present.

Diversity Pattern and Sampling Error

The analysis of the data suggests that the diversity of this fauna is essentially sympatric, because no indication of geographic or ecological replacement of species was found. There are no obvious barriers to dispersal; the forest cover is homogeneous, and the streams in the study area are 5 m wide at most. However, the concept of sympatric diversity is difficult to apply (De Winter, 1995; Emberton, 1995). This holds especially for rainforests, where it is almost impossible to find "restricted habitats with a homogeneous set of dominant plant species" (Solem, 1980). Although the low overall density of snails in this area is undoubtedly an effect of the low pH and the low mineral content of the soil, the actual numbers of live collected snails seemed to be very much dependent on weather conditions. The greatest numbers of live specimens were obtained during damp, warm conditions, as occur after heavy rains in the night and early morning followed by hot, sunny weather. After several days without precipitation rather few live snails were found, but during rain sampling was also less successful.

Dry conditions especially had a negative effect on the numbers of (semi)arboreal snails collected, due to problems in finding the sites where the snails hide. Solem et al. (1981) reported that some shelled arboreal taxa seal themselves firmly to the vegetation during dry periods, and in hindsight it seems possible that we not always applied enough force to shake these from their resting sites. Other species, notably slug-like taxa, probably seek shelter in holes and fissures of tree trunks.

The effect of climatic conditions is best illustrated by considering the data of the most diverse plot, Sta022, where 45 species were collected during a single visit. The richness of this plot was due to an exceptionally large number of specimens and species collected from the vegetation during optimal weather conditions as described above. The snail numbers found in the vegetation were much greater than on the floor, and the number of species found in both habitats was the same (Table 1). The number of species collected from the floor was not excessive, and several relatively common species were not represented. Under favourable conditions and by taking greater leaf-litter samples, it should be possible to find perhaps as much as 75% of the entire malacofauna within a single 0.04 ha plot.

Thus, in view of high proportion of the total fauna that can be found in a few square meter of forest, sampling error—resulting from the large proportion of rare species, the low overall snail abundance, and the varying weather conditions during sampling—has very likely had a significant effect. The differences in species composition found among the sites sampled in the same season, as indicated by the values of Whittaker's *I*, are therefore likely to be inflated. Geographic replacement of taxa also would seem unlikely in view of the small size and overall homogeneous nature of the study area. Sampling needs to be done at a much finer scale in order to detect differences in microhabitat preferences among species. Sampling error constitutes a serious problem for quantitative studies in these forests. Timed searching, as recently advocated by Emberton et al. (1996), does not seem to solve the problem, because it will inevitably result in overlooking even more species, especially the tiniest ones.

Streptaxid Diversity

The very large proportion of carnivorous species (all Streptaxidae) in a land snail fauna is a remarkable phenomenon, which is unique to the Afrotropical region as far as known. In the Manakau Peninsula, New Zealand, only four out of 72 species are carnivores, all belonging to the Rhytididae (Solem et al., 1981). The rainforest fauna of Manombo Reserve, Madagascar, has eight (15%) streptaxid species. Substantial proportions of Streptaxidae have been reported for much larger areas elsewhere in Africa, such as the former Belgian Congo (Pilsbry, 1919) and East Africa (Kenya, Tanzania and Uganda; Verdcourt, 1983). On a smaller geographic scale the proportion of streptaxid species seems to vary greatly. Tattersfield (1996) found nine (18%) streptaxids out of 50 land snail species in Kakamega Forest in Kenya, whilst in eastern Tanzania the proportion of Streptaxidae increased with altitude from about one fourth of the species below 500 m to 46% at a single station at 1000 m, taking up to one third of the collected individuals (Emberton et al., 1997).

The conspicuous radiation of the Streptaxidae contributes substantially to the species diversity here and elsewhere in tropical Africa. Maybe these carnivorous snails occupy a segment of the ecological space filled by nonmolluscan invertebrates outside the Ethiopian region. However, any data supporting this speculation are completely lacking. At present, no satisfactory explanation for this high proportion of carnivorous snails can be offered.

Emberton et al. (1997) surmised that "surely many of these streptaxid species must take nonmolluscan prey". However, in the course of six months of fieldwork in Cameroon, various streptaxid species have been only found feeding on other land snails or (in one occasion) their eggs. These incidental observations show that at least some species are not selective with respect to the species and size of their prey. *Edentulina liberiana,* for example, was found to attack some ten species of snails and semi-slugs (including observations from sites in Cameroon not described in this report), some up to twice its size. However, the considerable size-range of the streptaxids in this fauna (adult shell height 1.5–37.4 mm) is suggestive of quite some variation in feeding habits. Theoretically, Streptaxidae could live as scavengers on carrion, because at least two reports (Berry, 1963; Aiken, 1981) claim that some species feed in captivity on (mammalian) liver.

Shell Size and Shape

The malacofauna of block i2 occupies an enormous shell size range, but the vast majority of the species are rather small. Emberton (1995) provided shell size distributions of three diverse sympatric faunas, using shell diameter as an index of shell size. The shell diameter distribution reported here strongly resembles that found in the Manombo rainforest, Madagascar. The proportion of "minute species" (*sensu* Emberton, 1995; D between 0.5–5 mm) is virtually identical (66%), and in both faunas giant species (D > 40 mm) are represented. The other two faunas (Pine Mountain, U.S.A, and Waipipi Reserve, New Zealand) have very different size distributions. In New Zealand, 85% of the species are minute, and the remaining species are all smaller than 10 mm. In the U.S.A., giant species are lacking, and minute taxa constitute only 40% of the total fauna, the remaining species being approximately evenly distributed among the size classes.

Peake (1968) found in Solomon Island rainforests that ground-dwelling snails have a much more restricted shell-size range with generally smaller shells than arboreal or partly arboreal species. Here we observed that shells of species regularly exceeding 50 mm in height occur only in the arboreal and "indifferent" taxa. However, giant species (all Achatinidae) constitute a minor proportion of the total fauna, and shell dimensions of floor-dwelling and (partially) arboreal taxa were not different statistically.

The shape distribution of land snail shells was analysed by Cain (1977, 1978a, b, 1980) for a number of faunas. He observed that in most faunas species have shells that are either clearly higher than wide or wider than high, comparatively few having shells with approximately equal height and width. Cain (1978b: 219) suggested that species with high-spired shells tend to forage on vertical surfaces, and hence occur especially on rock faces and in trees; taxa with low-spired shells were hypothesized to feed more commonly on horizontal surfaces, and species with shells of about equal height and width to show little preference.

The distribution of H:D ratios of the shells found in this study deviates from those in the three sympatric faunas discussed by Emberton (1995). There are relatively many high-spired species, even more than in Madagascar, including some species in the 4.0–4.4 class, which is absent in Emberton's material. This is mainly due to the large proportion of subulinid species in the area studied. Another remarkable characteristic of this fauna is the very large proportion of shells in the 0.8–1.2 ("globose") class, and the apparent deficit of species in the 1.2–1.6 class. In the other three sympatric faunas, as well as in most large-scale faunas studied by Cain, the shell shape distribution is characteristically bimodal due to a deficit of globose-shelled snails. Most globose-shelled species are helicarionoids, especially of the heterogeneous genus *Trochozonites*, the 13 members of which have pyramidal shells, and tend to have arboreal habits, comprising only one true floor-dwelling species.

Cain (1978a) reported a relatively high proportion of globose species in the Helicostylinae of the Philippines and the Papuininae of the New Guinean area, most of which are arboreal species in rainforests. Emberton (1995) found arboreal species in a Madagascan rainforest to be globose rather than high-spired. Thus, perhaps there is some tendency in rainforest areas for globose-shelled species to have arboreal habits.

The suggestion that there might be a correlation between shell shape and preferred habitat has received experimental support for some British species (Cain & Cowie, 1978; Cameron, 1978, 1981; Cook & Jaffar, 1984), but does not seem to hold for high-spired Malagasy snails (Emberton, 1995), nor for the species studied here. Differences in shell shapes between geographically separate faunas generally appear to have a stronger taxonomic bias, like the great diversity of the high-spired Subulinidae in tropical Africa.

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